Plant and Soil **190**: 169–178, 1997.

Chemistry and microbial activity of forest and pasture riparian-zone soils along three Pacific Northwest streams

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Received 26 March 1996. Accepted in revised form 25 January 1997

Key words: denitrification, microbial biomass, riparian soils, soil respiration

Abstract

Throughout the United States, agricultural practices are responsible for large quantities of nutrients entering lakes and streams. Previous studies have shown that forested riparian areas can filter nutrients from surface runoff and groundwater that may potentially contaminate lakes and streams. This study examined seasonal differences in soil chemistry and soil microorganisms in paired mixed-forest riparian and pasture systems, the aim being to gain understanding of the sequestering of N and P. The forest soils retained higher levels of organic C and N, mineralizable N, extractable P, and fungal biomass, and had higher respiration rates than pasture soils. These findings suggest that forested riparian zones have a greater capacity than pasture soils to sequester C and retain nutrients. In past studies, fungal biomass has been shown to be less than bacterial biomass in grassland soils, but in this study, fungal biomass was greater than bacterial biomass throughout the year in both forest and pasture soils.

Introduction

There is considerable interest in using riparian ecosystems between agricultural land and streams or rivers as buffers against N and P pollution from non-point sources. Integral to this concept is the influence of riparian vegetation on groundwater chemistry, soil chemistry, and soil microbial communities. As groundwater moves through riparian areas, NO_3^- can be removed (Jacobs and Gilliam, 1985; Lowrance, 1992; Lowrance et al., 1984; Peterjohn and Correll, 1984) both by the action of denitrifying microorganisms (Lowrance et al., 1995) and by vegetative uptake (Ambus and Lowrance, 1991).

Within a given climatic zone or ecoregion, the amount of organic matter stored in soil and vegetation increases with time from the last catastrophic disturbance (Harmon et al., 1986; Perry, 1994). In most ecoregions, forests predominate in later stages of succession; thus the level of nutrients in forests is normally higher than that in grasslands (Entry and Emmingham, 1995). In addition, the fungal component of the soil foodweb builds as succession proceeds (Ingham et al., 1989; Ingham and Thies, 1996; Singh and Singh, 1995). In past assessments of the effects of riparian vegetation on nutrient cycling and groundwater chemistry, investigators have shown that riparian forests are more effective than agricultural row crops in removing nutrients from near-surface groundwater (Lowrance et al., 1984).

The general objective of this study was to assess the impact of forest and pasture vegetation on riparian soil processes by measuring differences in soil chemistry and microbial biomass activity. Specifically, changes in levels of organic C, total and mineralizable N, extractable P, and microbial activity and numbers were assessed in paired forest-pasture systems over one seasonal cycle.

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Materials and methods

Site descriptions

Soil samples from forested and pasture plots were taken in the Willamette Valley near Corvallis, Oregon, USA, from three riparian sites: along Oak Creek on the Oregon State University Dairy Farm (lat. 44°30'), along Jackson Creek on MacDonald State Forest (lat. 44°38'), and along Soap Creek on Dunn State Forest (lat. 44°41'). PH values and seasonal temperature and moisture data for the ripirian soils used in this study have been published elsewhere (Entry et al., 1994). The soil pH ranged from 5.8 to 6.3. The mean annual temperature for these soils ranged from 10° to 12° C for all sites. At any given season, the soil temperature and moisture values were essentially the same for all sites, with few differences noted between forest and pasture soil temperatures. With the exception of the summer, when forest soils had more moisture than the pasture soils, soil moisture content was also essentially the same in forest and pasture soils (Entry et al., 1994). All sites are more than 70 m above sea level, with slopes of 3–8%, 100–150 cm precipitation per year ($\leq$ 2% occurring as snowfall), and a frost-free season of 165–210 days (Knezevich, 1975). Active decomposition occurs in soils throughout the generally mild winter. Summers are generally dry (below 5% soil moisture), and microbial activity is lower at that time than throughout the rest of the year. The forests have closed canopies of 40-year-old trees. The pastures have been grazed lightly by sheep, cattle, and deer over the last 40 years, after heavy grazing from 1850 to 1950.

The Oak Creek soil is a Fluvaquentic Haplaquoll, fine mixed mesic in the Waldo series (Knezevich, 1975). Vegetation in the forest area is *Quercus kelloqii* Newberry, *Rosa woodsii* Lindl., and *Rubus parviflorus* Nutt.; vegetation in the pasture area is *Festuca arundinacea* Schreb, *Trifolium pratense* L., and *Lolium perenne* L.

The Jackson Creek soil is a Vertic Haploxeroll, fine montmorillonitic, mesic in the Witham series (Knezevich,1975). Vegetation in the forested area is *Pseudotsuga menziesii* (Mirb.) Franco, *Q. kelloggii, Rosa woodsii, Rubus parviflorus,* and *Polystichum munitum* (Kaulf.) Presl.; vegetation in the pasture area is *F. arundinacea, T. pratense,* and *L. perenne.*

The Soap Creek soil is a Cumulic Ultic Haploxeroll, fine silty mixed mesic in the McAlpin series (Knezevich, 1975). Vegetation in the forest area is *Pseudotsuga menziesii, Q. kelloggi, Symphocarpus albus, R. parviflorus,* and *P. munitum;* vegetation in the pasture area is *F. arundinacea, T. pratense,* and *L. perenne.*

Soil sampling and processing

Four mineral soil samples were taken at each arbitrarily selected site to a depth of 10 cm within the mineral soil (soil litter and "O" horizon materials were removed before sampling). Soil was placed in zip-lock plastic bags and transported to the laboratory in an ice chest. Testing for mineralizable N, microbial activity, and soil moisture was initiated within 24 h of collection. The soils were held at 4 °C between collection and analyses. Samples were collected on the first week of the months of January (winter), May (spring), August (summer), and November (fall). All soils except those used for biomass determinations were sieved through a 2-mm mesh stainless steel sieve prior to processing. The 59 unsieved soil samples used in the biomass measurements had all visible roots and rocks removed by hand.

Soil chemical measurements

Organic C was estimated by dry ashing (Nelson and Sommers, 1982). Concentrations of total N, NH_4^+, mineralizable NH_4^+, NO_3^-, and acid-soluble P were measured. Organic N was determined by the micro-Kjeldahl technique described by Bremner and Mulvaney (1982); extractable concentrations of NH_4^+ and NO_3^- were determined in soils treated with 2 *M* KCl (Keeney and Nelson, 1982).. Acid-soluble P was determined in soils treated with a Bray extraction (Olsen and Sommers, 1982). These extracts were analyzed by using colorimetric methods on a series 300 rapid flow analyzer (Alpkem). The amount of N mineralizable under anaerobic conditions was determined by incubating 10 g of field-moist soil in 57 mL screw-top test-tubes filled with deionized water and then sealed (Griffiths et al., 1990). The tubes were incubated for 7 days at 40 °C. Mineralized N was calculated as the difference between NH_4^+ present before and after incubation (Corning NH_4^+ electrode).

Microbial variables

Active and total fungal biomass were estimated with methods described by Lodge and Ingham (1991). One gram of soil was first suspended in 9 mL of sterile tap water, and then 1 mL of the suspension was removed

and stained with fluorescein diacetate (Sigma Scientific Co.) for 3 minutes. One mL of 1.5% water agar was added to the stained suspension and an aliquot placed in a well of two adhering coverslips 1 cm apart on a microscope slide. A coverslip was placed over the stained agar suspension, and the samples were placed in a humidifier to prevent agar dehydration.

Active fungal biomass was estimated by measuring the length and width of all fluorescent hyphae within a transect of the agar film (250 total magnification). To assess within-sample variability, the length of all active hyphae in three transects was measured. Active bacterial biomass was estimated by counting all fluorescent bacteria in a microscope field (450 total magnification). Numbers, legth, and diameters of bacteria were noted, and all active bacteria in five fields were counted to assess within-sample variation.

Total fungal biomass was estimated by measuring the length and diameter of hyphae in 3 to 60 fields with phase-contrast microscopy (100 total magnification). Three measurements were made to assess within-sample variability. Active and total bacterial biomass were estimated by staining 1 mL of 1:100 soil dilution with fluorescein isothiocyanate (FITC; Sigma Scientific Co.), as described by Babiuk and Paul (1970). The suspension was filtered onto a black polycarbonate filter (0.2 μm diameter pore size, Poretics Corp.), and all fluorescent bacteria in each of ten fields per filter were counted. Total bacterial biovolume per gram dry weight of soil was estimated from the mean number of bacteria per field, their average diameter and length, and the dilution and area per field.

Biovolume was calculated from measurements of length and width of fungi and bacteria. Once biovolume was calculated, biomass was estimated by using a conversion factor of 130 mg C mm^{-3}, which assumes a wet density of 1.1 g cm^{-3}, 0.25 dry-matter content, and 0.37 C content in the fungus or bacterium (Jenkinson and Ladd, 1981).

Denitrification potential and respiration rates were measured as described by Griffiths et al. (1990), except that they were measured at 25 °C. To measure denitrification potential, 5 g of field-moist soil was added to each 25-mL Erlenmeyer flask, which was stoppered, purged with Ar for 4 min at 200 mL min^{-1}, and then injected with 2 mL of a solution containing 1 m*M* glucose and 1 m*M* $NaNO_3$. The concentration of N_2O in the headspace after a 2-h incubation period was measured with a gas chromatograph (Hewlett Packard model 5730A) fitted with an electron capture detector. The integrator was calibrated with standard gases as an external standard. Time-course measurements of selected samples showed that the N_2O production rate was constant over the incubation period. A replicate run was made with one-third of the samples, chosen arbitrarily, in a 10% C_2H_2 atmosphere in order to inhibit reduction of N_2O to N_2. The amount of N_2O produced was the same with or without added 10% C_2H_2 in the headspace.

Respiration rates were determined by monitoring CO_2 concentrations in the headspace of 25-mL Erlenmeyer flasks containing 5 g of fresh field-moist soil. The CO_2 concentration was determined by gas chromatography at 0 and 2 h, as previously reported by Griffiths et al. (1990).

Statistical analysis

All dependent variables were tested for normal distribution, and those not normally distributed were log-transformed before analysis. Data were then analyzed as a randomized block design in SAS (SAS Institute, Inc., 1982). Residuals were equally distributed with constant variances. Except where indicated, all values are expressed per gram dry weight of soil. Difference between mean values was determined with Fisher's protected least significant difference at the level $p < 0.05$. The data were analyzed for two-way interactions between site and treatment. Significance of linear correlations was calculated by the Spearman rank-correlation method.

Results and discussion

Carbon and nitrogen

Organic C and N are higher in forest soils than in pasture soils, with the organic N significantly higher in forest than pasture soils throughout the year (Figure 1). The peak winter organic N in the forest may be the result of N in fall litter inputs being incorporated into fungal and bacterial biomass through decomposition and then moved into deeper layers by arthropods and earthworms during the winter (Lee, 1985; Scheu and Wolters, 1991). Temperatures in the Willamette Valley rarely drop to freezing during the winter, and soil under litter layers in the forest, or in thick grass coverage in the pasture, does not freeze. Invertebrates remain active through the entire winter, moving down in the soil profile to escape cold days.

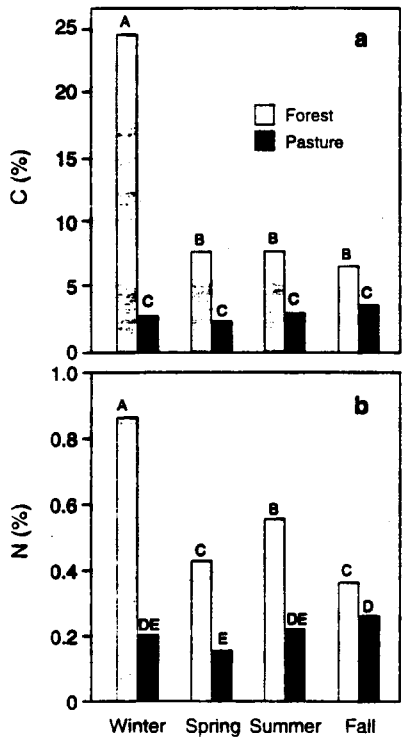

Figure 1. Mean values (three sites combined) for organic (**a**) C and (**b**) N as a percentage of total soil weight, by season. Analysis of variance showed interactions of vegetation type and season. The same letters indicate no significant difference at $p < 0.05$.

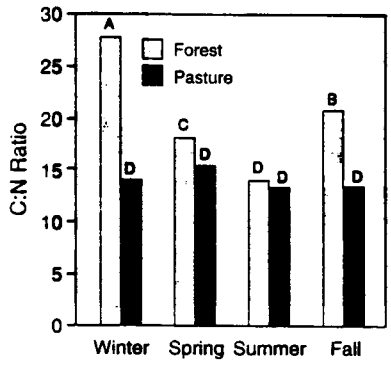

Figure 2. Mean values (three sites combined) for C:N ratios, by season. Analysis of variance showed interactions of vegetation type and season.

Except in fall and winter forest soils, C:N ratios in both soils were relatively constant throughout the study (Figure 2). The increased ratio in the fall forest C:N may reflect the input of oak leaves (with typical C:N ratios of 100 to 150) into soil that in summer had a C:N ratio of 15. Studies of deciduous hardwood forests have shown that during a 1-month period in the fall, there is a peak of carbon input into the forest that is equivalent to >80% of the annual above-ground and 20% of the below-ground input (Hendrick and Pregitzer, 1993; Pregitzer and Burton, 1991); a similar input could be occurring in the oak-dominated riparian forests used in this study. The litter generated during this period could be incorporated into the mineral soil by earthworms found in these soils (Lee, 1985; Scheu and Wolters, 1991). By the time the soils were resampled in spring, the C:N ratios were once again lower, most probably because of normal litter decomposition in which N generally is conserved as it is incorporated into microbial biomass and recalcitrant humic pools during decomposition. As N is conserved, C is mineralized to CO_2, resulting in lower C:N ratios (Paul and Clark, 1989).

Extractable NH_4^+ and NO_3^- were not highly correlated with mineralizable N in forest soils (Table 1), but they were highly correlated in pasture soils (Table 2). Extractable NH_4^+ and NO_3^- are measures of N in soil pools at the time soil is collected. Mineralizable N is that portion of organic N that is readily mineralized under anaerobic conditions during a 7-day incubation. A relationship between extractable inorganic forms of N and mineralizable N was not expected.

It has been suggested that mineralizable N may, under certain conditions, reflect the level of microbial biomass (Myrold, 1987). In forest soils there was significant positive correlation between mineralizable N and both active fungal and active bacterial biomass (Table 1), but this was clearly not the case in the pasture soils (Table 2). We cannot determine from these data whether a significant portion of the mineralizable N is actually in the form of active microorganisms or whether the microorganisms are active because there is readily utilizable organic N present. Mineralizable N reflects the labile organic N pool from which NH_4^+ and NO_3^- are generated, but the patterns observed in cycling were very different in the forest than in the pasture (Figure 3a, b, c). Mineralizable N and extractable N pools were somewhat correlated in the pasture but not the forest soil (Tables 1 and 2).

Seasonal comparison of extractable NH_4^+ and NO_3^- in forest and pasture soils shows that in forest soils mineralizable N and NH_4^+ concentrations decreased from spring to summer and NO_3^- increased, whereas they fluctuated in tandem in pasture (Figure 3a, b, c). Higher summer NO_3^- concentrations in forest and pasture soils may be caused by lower denitrification rates,

Table 1. Spearman rank correlations for all variables in forest soils

	Respiration	Denitrification	Organic C	Organic N	Mineralizable N	Extractable P	CEC[b]	Total biomass		Active biomass		C:N ratio	Extractable	
								Fungal	Bacterial	Fungal	Bacterial		Ammonium	Nitrate
Respiration	1.000	0.373	0.038	0.054	0.122	-0.018	-0.178	0.614**	-0.402*	0.250	0.373	-0.252	-0.336	-0.276
Denitrification		1.000	-0.231	-0.238	0.550**	0.089	-0.284	0.150	-0.178	0.418*	0.546**	-0.343	0.206	-0.015
Organic C			1.000	0.984***	-0.097	0.184	0.616**	0.278	0.118	-0.049	-0.313	0.613**	-0.360	0.016
Organic N				1.000	-0.061	0.189	0.609**	0.294	0.138	-0.036	-0.322	0.588**	-0.393	0.051
Mineralizable N					1.000	0.291	-0.400*	0.173	-0.093	0.426*	0.401*	-0.458*	0.426*	0.477*
Extractable P						1.000	0.276	0.165	0.229	0.112	0.256	0.154	0.376	0.148
Cation exchange capacity							1.000	-0.307	0.609**	-0.386	-0.141	0.880***	-0.200	0.0800
Total fungal biomass								1.000	-0.660***	0.435*	0.055	-0.323	-0.187	-0.172
Total bacterial biomass									1.000	-0.336	0.072	0.594**	0.159	0.213
Active fungal biomass										1.000	-0.010	-0.565**	0.341	-0.106
Active bacterial biomass											1.000	-0.141	0.175	0.190
C:N ration												1.000	-0.244	0.104
Ammonia													1.000	0.268
Nitrate														1.000

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 2. Spearman rank correlations for all variables in pasture soils

	Respiration	Denitrification	Organic C	Organic N	Mineralizable N	Extractable P	CEC[b]	Total biomass		Active biomass		C:N ratio	Extractable	
								Fungal	Bacterial	Fungal	Bacterial		Ammonium	Nitrate
Respiration	1.000	-0.001	-0.077	-0.092	0.099	0.372	0.270	0.492*	-0.167	0.110	-0.091	-0.188	0.075	0.110
Denitrification		1.000	-0.177	-0.240	0.066	0.054	-0.333	0.171	-0.174	0.448*	0.322	0.165	0.012	0.090
Organic C			1.000	0.967***	0.637**	0.435*	0.293	-0.277	0.485*	-0.059	0.287	-0.236	0.404	0.548**
Organic N				1.000	0.629**	0.435*	0.221	-0.312	0.423*	-0.176	0.191	-0.305	0.498*	0.586**
Mineralizable N					1.000	0.637***	0.056	-0.264	0.152	-0.047	0.231	-0.212	0.677***	0.878* **
Extractable P						1.000	0.303	-0.170	0.350	0.095	-0.004	-0.482*	0.663***	0.657***
Cation exchange capacity							1.000	-0.250	0.644**	-0.330	-0.167	-0.150	-0.102	-0.088
Total fungal biomass								1.000	-0.411*	0.479*	0.137	0.213	-0.109	-0.226
Total bacterial biomass									1.000	0.152	0.288	-0.191	0.125	0.013
Active fungal biomass										1.000	0.404*	0.406*	0.079	0.007
Active bacterial biomass											1.000	0.182	-0.070	0.038
C:N ration												1.000	-0.342	-0.318
Ammonia													1.000	0.788***
Nitrate														1.000

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

low leaching rates, and reduced nutrient demand by vegetation during summer drought, or perhaps by less immobilization due to reduced microbial activity during drought, as hypothesized by Luizao et al. (1992). The same phenomenon might explain the increase in extractable P seen at the same time in forest and pasture soils and the buildup of NH_4^+ in pasture soils. Summer denitrification rates were the lowest for the year (Figure 4), as other researchers have repeatedly observed (Davidson and Swank, 1987; Parsons et al., 1991; Vermes and Myrold, 1992).

There have been reports that concentrations of NH_4^+ and NO_3^- are generally different in forest and grassland soils (Binkley et al., 1992; Hunt et al., 1988; Ingham et al., 1989; Neill et al., 1995). Ammonium appears to be the common form of inorganic N in conifer forest soils and NO_3^- in grassland soils. In most conifer forest soils, where there is a lack of nitrifying bacteria, mineralized N is not rapidly converted to NO_3^-, resulting in a buildup of NH_4^+, which is less likely to be removed from soils by leaching. When organic N is mineralized in grassland soils (Ingham et al., 1989), however, the NH_4^+ released generally is rapidly converted to NO_3^- by nitrifying bacteria. Deciduous forests appear to be intermediate: NO_3^- concentrations in alder and poplar soils are usually higher than NH_4^+ (Perry, 1994), while the reverse is true for maple (*Acer*), beech (*Fagus*), and oak (*Quercus*) soils. The forest plots used in this study had equal densities of oak (*Q. kelloggii*) and Douglas-fir (*P. menziesii*). These mixed deciduous-conifer stands next to pastures appear to be on the continuum between NH_4^+ -dominated conifer soils and NO_3^- -dominated grassland-deciduous soils. Other researchers have observed similarly "atypical" situations in similar stands (McClellan, 1987; Perry, 1994).

Winter mineralization of organic N to NO_3^-, which is then drawn down by increased denitrification, microbial immobilization, and plant uptake, may account for the reduction in total N in the spring. This phenomenon was considerably greater in forest than in pasture soils, where the seasonal difference was not statistically significant. This suggests that there may be greater turnover of organics in forest soils than in

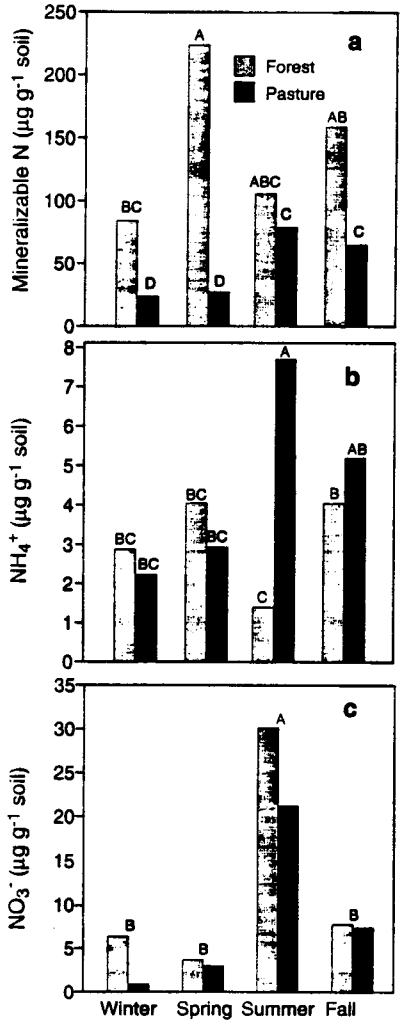

Figure 3. Mean values (three sites combined) for (a) mineralizable N and extractable (b) NH_4^+ and (c) NO_3^- in $\mu g\ g^{-1}$ dry weight of soil, by season. Analysis of variance showed interactions by season only for NO_3^-.

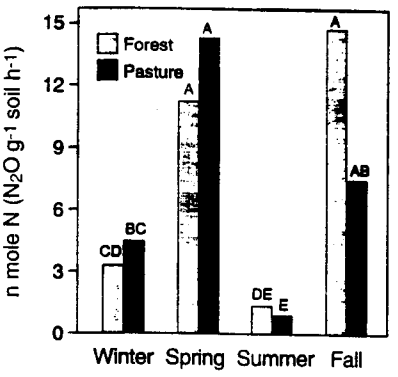

Figure 4. Mean denitrification rates (three sites combined) in nmole N as nitrous oxide g^{-1} dry weight soil h^{-1}, by season. Analysis of variance showed intractions by vegetation type and season.

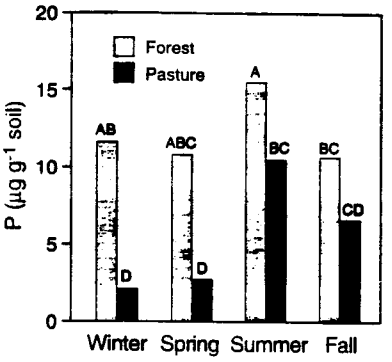

Figure 5. Mean values (three sites combined) for acid-soluble P in soil, by season. Analysis of variance showed interactions of vegetation type and season. The same letters indicate no significant difference at $p < 0.05$.

pasture soils, a hypothesis supported by the values for organic C (Figure 1), which show essentially the same trend.

Acid-soluble phosphorus

In all seasons except fall, acid-soluble P was significantly higher in forest than in pasture soils. Forest soils showed relatively little seasonal variability in acid-soluble P concentrations in comparison with pasture soils, which suggests that forest soils may better buffer seasonal shifts in the sources and sinks of acid-soluble P (Figure 5). In pasture soils, acid-soluble P concentrations were lowest in winter and spring and highest in summer. A previous study of nutrients similarly showed greater concentrations of organic P in forest litter than in grassland litter (Entry and Emmingham, 1995). Since most P is in the organic form in these forest soils (Stewart and Tiessen, 1987), it is likely that the soils are capable of storing more P in all forms than comparable pasture soils. The elevated P concentrations in the litter and soils may reflect the capacity of riparian forests to trap P in polluted groundwaters (Lowrance et al., 1984; Pinay, 1986).

There was high correlation of acid-soluble P with total C and N, mineralizable N, and extractable NH_4^+ and NO_3^- concentrations in pasture soils (Table 2), but not in forest soils (Table 1). The reason for these correlations is not known, but in the forest, extractable P peaked when fungal activity was at a minimum, whereas in the pasture, P was more extractable at the same

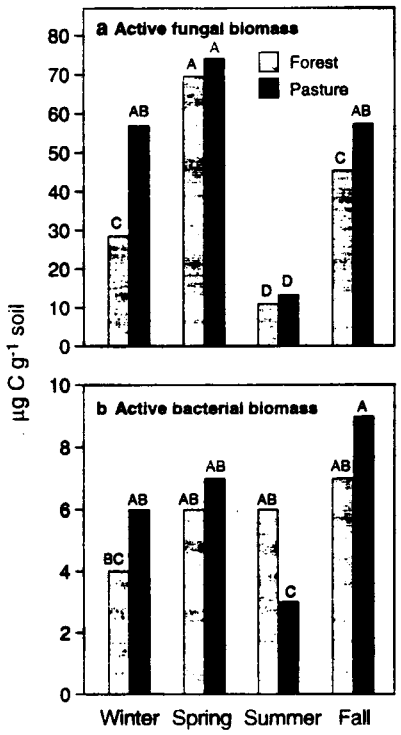

Figure 6. Mean values (three sites combined) for active (**a**) fungal and (**b**) bacterial biomass as μg C g^{-1} dry weight soil, by season. Analysis of variance showed interactions of vegetation type and season.

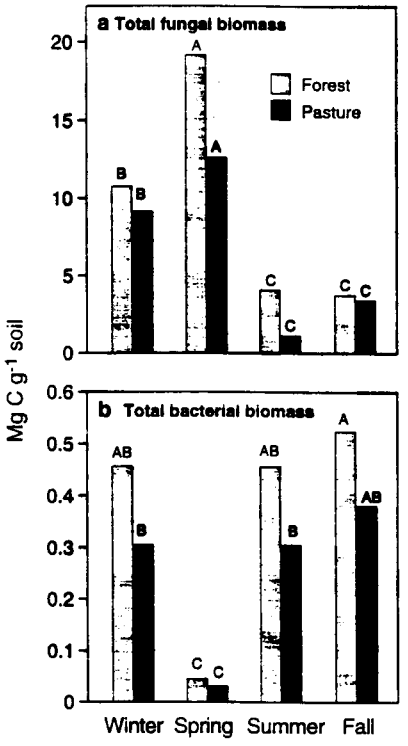

Figure 7. Mean values (three sites combined) for total (**a**) fungal and (**b**) bacterial biomass as mg C g^{-1} dry weight soil, by season. Analysis of variance showed interactions of vegetation type and season.

time active bacterial biomass dipped significantly (Figures 1, 6).

Microorganisms

Active fungal biomass was significantly lower in forest than in pasture soils in winter and fall, but essentially the same in both vegetation types during the rest of the year (Figure 6). Active fungal biomass was lowest in summer, perhaps reflecting dry conditions. Except in summer, active bacterial biomass showed no significant differences between forest and pasture soils (Figure 6).

Prior work has shown that the microbial communities of coniferous forest soils are dominated by fungi, while grassland soils are generally dominated by bacteria (Ingham et al., 1989; Ingham and Horton, 1987; Ingham and Thies, 1996). Our study shows that total fungal biomass was far greater than total bacterial biomass in both forest and pasture soils (Figure 7); thus the previous observations that NH_4^+ is the primary form of inorganic fixed N in forest soils and that pasture soils are dominated by bacteria do not seem to hold in these riparian soils. However, Neely et al. (1991) reported that fungi were more important than bacteria in decomposition processes in a river-bottom agricultural study in Georgia. Further work is needed to assess the gradient of fungal:bacterial biomass and NO_3^-:NH4 ratios in riparian soils under different vegetation.

Interestingly, a negative correlation between fungal and bacterial biomass in both forest and pasture soils ($r = -0.66$ and -0.41, respectively) was demonstrated in the seasonal data: spring fungal biomass was elevated, but bacterial biomass was depressed (Figure 7). The reverse trend was seen in summer and fall. To our knowledge, this is the first report in the soils literature of a negative correlation between fungal and bacterial biomass for forest ecosystems; however, the effect has been observed in grasslands (Ingham et al., 1989).

Another indicator of total microbial activity that integrates a range of metabolic transformations in soils is respiration under laboratory conditions without the presence of active roots. Not surprisingly, the forest

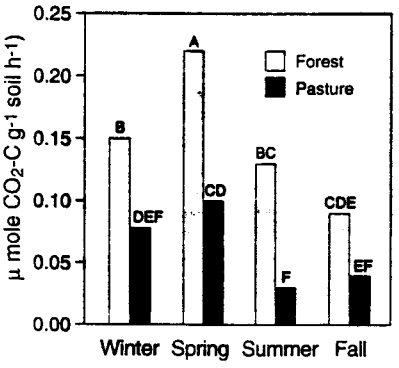

Figure 8. Mean soil respiration (three sites combined) in μmole CO_2-C g^{-1} dry weight soil h^{-1}, by season. Analysis of variance showed interactions of vegetation type and season.

soils showed consistently higher respiration rates than pasture soils because of the higher fungal and bacterial biomass and organic C found in forest soils (Figure 8). Forest soils showed the lowest rates in fall and pasture soils the lowest rates in summer. Both soils showed significant differences between spring and summer. The strong positive correlation between soil respiration and total fungal biomass in both forest and pasture soils links soil respiration to fungi. The negative correlation between respiration and total bacterial biomass suggests not only that more soil respiration is attributable to fungi, but also that fungi and bacteria may have a functional antagonism in these riparian forest soils (Tables 1, 2).

Forested riparian soils can significantly reduce NO_3^- concentrations in both shallow and deep groundwater (Haycock and Pinay, 1993; Jordan et al., 1993; Lowrance et al., 1984; Nelson et al., 1995; Osborne and Kovacic, 1993). Three mechanisms are possible: plant uptake, microbial immobilization, and denitrification. Because of the potentially important role of denitrification in the removal of NO_3^- from groundwater, a number of studies have focused on riparian denitrification (Ambus and Lowrance, 1991; Groffman et al., 1991; Lowrance, 1992; Schipper et al., 1993). In our study, denitrification potentials in forest and pasture riparian zones were highest in spring and fall and lowest in summer (Figure 4), most likely controlled by plentiful moisture availability in the spring and fall and draughty conditions in the summer. Lowrance (1992) also found seasonal differences in denitrification potential, with the highest rates observed from late August to early December and the lowest rates from February to June. In addition, he observed that denitrification potential was relatively high in surface soils (the top 10 cm), but low in deeper water-saturated soils. He concluded that denitrification did not account for reductions in saturated-zone NO_3^- but could account for reductions in the shallow groundwater NO_3^- as it flowed through riparian soils (Lowrance, 1992). An alternative explanation for the rapid reduction in NO_3^- levels in riparian-zone groundwater is that the N-filtering capacity of riparian forests may be due to N sequestration in leaf litter and fine roots (Haycock and Pinay, 1993; Lowrance, 1992).

In a study of winter groundwater NO_3^- dynamics in poplar and grass floodplains, Haycock and Pinay (1993) found that both buffer strips could retain NO_3^- even when there was no vegetative growth, suggesting that microbial processes (both nutrient immobilization by microorganisms and denitrification) driven by litter carbon may be the primary mechanism by which NO_3^- is removed by groundwater in the winter. The increase in microbial metabolism as reflected in elevated respiration rates and increased total fungal biomass from fall through spring suggests that microbial immobilization may be a factor in nutrient retention in riparian zones during periods of low plant nutrient demand.

It is not known whether planted riparian filter belts can achieve the same effects as native riparian forests. More work is needed before the potential of forested riparian zones for buffering streams from groundwater contamination is well understood. In this study, organic C, total N, mineralizable N, acid-soluble P, and total fungal and bacterial biomass were all greater in forest riparian soils than in pasture soils. These observations, along with those reported in another study (Entry and Emmingham, 1995), suggest that forest soils have a better nutrient-retaining capacity than riparian pasture soils.

Acknowledgements

The technical assistance of Bruce Hanson, Nadine Wade, and Carol Glassman is gratefully acknowledged. We thank the National Science Foundation for financial support from grants BSR8717849 and BSR9106784.

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Section editor: R Merckx